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SHORTER ARTICLES AND DISCUSSION

THE MENDELIAN VIEW OF MELANIN FORMATION

Apparently there is no danger that the biological world will suffer permanent paralysis as the result of general acquiescence in hypotheses which have recently gained wide acceptance but for which fundamental proof seems not to be forthcoming. Especially is this the case when biologists whose special fields of work give them only an incidental interest in Mendelian and de Vriesian affairs will take the trouble to attach their batteries to the wires leading into the Mendelian field in order to counteract the paralyzing effect of what they regard as intellectual poison. I am a firm believer in the value of scientific trespass. Very frequently a group of scientists become moribund because they have no one to criticise them. An outsider who finds that his own work touches that of such a group may render real service by pointing out relations which those immediately concerned have overlooked and may thus cause readjustments of theory and hypothesis that are frequently much needed.

An excellent case of this kind is found in Riddle's interesting article in the *Biological Bulletin* for May, 1909.[1] One can hardly read this article without suspecting that Riddle is purposely somewhat extreme in his attack on the current interpretations of Mendelian phenomena in order to get a response from those who are responsible for these interpretations. It appears to the writer that Riddle attacks very successfully the de Vriesian interpretation of these phenomena. Unfortunately, however, he utterly confuses Mendelian facts with de Vriesian and Weismannian theories—hypotheses, rather, and attempts to throw both facts and hypotheses out of court. Riddle is not entirely to blame in this matter, however, for the de Vriesians generally have made the same mistake. If Riddle succeeds in arousing Mendelianists to a realization of the fact that the facts of Mendelian inheritance are not dependent on de Vriesian hypotheses he will have rendered a distinct service to biology.

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[1] "Our Knowledge of Melanin Color Formation and Its Bearing on the Mendelian Description of Heredity," Oscar Riddle. *Biol. Bul.*, May, 1909, pp. 316–351.

Mr. Riddle must not forget that we have a long list of incontrovertible facts that are not in disagreement with the facts of melanin production cited by him, and which are not dependent on any theory involving discontinuous variation, but which may be interpreted in such a way as to take cognizance of the ascertained facts of physiological chemistry. Riddle throws all "factor" hypotheses overboard, apparently under the impression that they all depend on the Weismannian doctrine of determinants. Fortunately, such is not the case. These hereditary factors are established facts, while the Weismannian conception of them is, in the writer's view, probably wholly wrong.

Riddle points out that the chromogens in animals are tyrosin and related aromatic compounds. Tyrosinase, an oxidizing enzyme, converts tyrosin into melanins. Fuerth and Schneider concluded that "tyrosinase-like ferments are widely distributed in the animal organism and probably always appear wherever and whenever a physiological or pathological formation of melanin occurs." Gessard showed that the presence of acids, alkalis and salts has a marked effect on the colors produced by the action of tyrosinase on tyrosin. Bertrand determined the type of substance, of which there are many representatives, which tyrosinase can oxidize to melanins. In the oxidizing process each of these substances are converted step by step through a series of colors before reaching the final stage. They vary somewhat as to initial and final colors, the early stages being lighter than the later. The series of colors usually runs from yellow to orange, proceeding onward to brown or black. Any benzine nucleus with a hydroxyl attached can be converted to a melanin by tyrosinase. Some substances have red or mahogany as the final stage reached in the oxidation process.

Riddle further points out that the facts of the pathological development of melanins show the dependence of tyrosin oxidation upon somatic conditions which may be of temporary, intermittent, or reversible character, but he assumes, without sufficient basis, that these facts preclude the possibility of accounting for observed phenomena of color inheritance on a basis of specific transmission and segregation in the germ cells. He seems to think that any kind of segregation in the germ cells necessarily implies pangenes, such as those proposed by de Vries, or determinants, such as those proposed by Weismann. It is easily shown that this is not the case. The facts of segregation are not at all inconsistent with the idea that melanin formation is in itself a generalized function of the cell. Cytological investigations during the past two or three decades lend support to the hypothesis that the cell is composed of a number of more or less definite organisms. Now the production of black pigment, for instance, may be a process in which every organ of the cell plays a part. Riddle has shown that the particular color of an organism, when this color is melanic in character, is due to the fact that the oxidation process stops at a more or less definite point. We may imagine that the relative quantity of tyrosin and tyrosinase present in the cell has something to do with the point at which the process terminates under normal conditions. Now if a single cell organ should, because of some change in its nature, fail to produce its usual measure of one of these necessary substances, we may easily imagine that the point at which the oxidation process would stop would be changed accordingly. Now if the cell organ which is responsible for this difference happens to be a chromosome, and if chromosomes behave in the reduction division as a great many cytologists believe they do, then we at once get the phenomenon of Mendelian segregation independent of any idea of unit characters at all. This idea will be further developed in another paper by the present writer.

Riddle continually draws conclusions that do not seem to be justified by the facts he states. For instance, he states that melanin formations, under certain pathological conditions, "indicate that for the building of any melanin at all the actual conditions of the organism or the organ have a rôle to play that is quite out of keeping with any 'once-for-all determinance' by the shuffling of color factors through the germs." This is not a necessary conclusion unless we think of color factors as definite organs in the cell. I have just pointed out that what we have been calling factors may really be only differences in function of cell organs. There is no doubt at all that, for the development of almost any peculiarity or character, local conditions in the organism are important factors, but they are not the only factors. There must have come through the germ cell certain tendencies before these characters could develop at all. The horns of cattle are a good illustration of this point. These organs develop only at certain points of the organism, but the tendency to develop them when the proper conditions are given in the organism is unquestionably a matter of inheritance, nor can there be any question that there is a Mendelian segregation with reference to this tendency. This does not mean, however, that there is a bullet somewhere in the germ plasm which is wholly responsible for the development of horns. I imagine that the development of horn tissue is a process in which probably all of the organs of the cell participate; but if there is one organ which has become so changed in its functions that it can no longer take its usual and necessary part in the development of these organs, and if this organ is a chromosome, then we necessarily get the phenomenon of Mendelian segregation in inheritance with reference to this character.

Riddle points out a good many facts that it is well for Mendelianists to keep in mind in formulating hypotheses to account for the facts they discover. One of the most interesting of these is the finding by Spiegler that the hair of white horses and the wool of white sheep contain a white melanin. Some investigations indicate that these white melanins represent a more advanced stage of oxidation than do black melanins. White of this character we should therefore expect to be dominant, in the Mendelian sense. Riddle suggests that in certain white birds, and I presume the same would apply to albinos generally, the oxidation is not carried far enough to produce color. In these cases we should expect white to be recessive, in the Mendelian sense.

That melanin production is at least frequently the result of a long series of reactions is strongly indicated by Fornier's experiments on tadpoles. By giving varying amounts of nutriment he was able to produce a series of colors in these animals ranging from white through gray, and finally from yellow to black. Apparently these results were due to the fact that in individuals insufficiently nourished the oxidation process ended at different points in the series of possible stages.

The writer has observed a similar phenomenon in the case of cow-peas. In varieties of these plants having highly colored seeds it is a frequent occurrence to find imperfectly developed seeds of lower color than perfectly developed ones. For instance, the black-seeded varieties occasionally imperfect seeds are found which are light brown, due, presumably, to the fact that the oxidation process in these seeds did not reach the stage normally reached in perfect seeds. It may be further noted that in cow-peas melanin production seems to occur only in the later stages of development.

From a few facts like those above stated Riddle makes the sweeping conclusion that "in an animal that produces melanin color there exists all the machinery necessary to produce a series or scale of these colors. What is actually produced is, in several demonstrated instances, dependent on the physiological state of the organism." It does not necessarily follow that this is true in all organisms, or even in all animals, though it must be admitted that such may be the case. There is a good deal of evidence that in some organisms the oxidation processes do not lead through a series of colors, such as Fornier found in tadpoles, but that when color begins to appear at all it is of a definite character and that we have variation only in the amount of that color present. It seems quite probable that in some organisms the mechanism present is limited to the production of a single color character, yet this is a matter for further investigation.

Even if there is only one process of oxidation and the series of reactions results in a graduated series of color pigments this does not necessarily imply that a tendency to a certain color is not purely hereditary and that it could not undergo the phenomena of segregation. The normal stage of oxidation reached in an organism may be an intermediate one, as in red cattle. If a single cell organ is responsible for the oxidation process stopping at this stage, and if that cell organ behaves as chromosomes appear to do at least in some organisms, then we would necessarily have the phenomenon of Mendelian segregation.

Riddle seems to labor under the impression that in order to explain the so-called Mendelian factors it is necessary to assume an indefinite number of specific enzymes or chromogens. I think I have already said enough to point out that this is not the fact. There is much evidence, however, that in the color of animals we do have at least three specific enzymes or chromogens, for we find three kinds of color material deposited in the same parts of the organism. Furthermore, the tendency to produce each of these three types of pigments has been demonstrated to be separately heritable.

Riddle points out the very interesting fact that Miss Durham[2] investigated the enzymes in the skin of black, chocolate, yellow, and albino mice, and reported finding enzymes for black, chocolate, and yellow. Riddle criticizes Miss Durham's conclusions for no other apparent reason than that they apparently oppose his views. In albinos Miss Durham was not able to decide definitely concerning the presence of enzymes but was of the opinion that the enzymes were not present. Riddle's suggestion that yellow is a blend between albino and black would be quite interesting if we did not know that it is not true. Castle has recently shown that the tendency to produce yellow pigment, in rabbits at least, is a separately heritable tendency. On the other hand, we can agree with Riddle's statement that the "data warrant the definite statement that yellow mice are forms with the power of oxidizing tyrosin compounds, to an intermediate point."

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[2] *Proceedings Royal Society*, Vol. 74.

If it were not for the well-established facts of segregation in the inheritance of color, Riddle's statement that "in gametic unions we deal not at all with factor particles but merely mix and amalgamate to various degrees powers of tyrosin oxidation and conditions supplied by the differentiations of tissues and organs, together with environmental conditions external and internal, supply whatever else is concerned in color production." It is really to be regretted that Riddle does not know more of the facts of color inheritance, for his incisive remarks indicate that if he knew these facts and took proper cognizance of them he would be highly useful to Mendelianists by way of developing an explanation of Mendelian phenomena more in keeping with the facts of physiological chemistry.

His criticism of Castle's work on rabbits is entirely unfounded. He assumes that the factors found by Castle can not exist apart from pangenes of the de Vriesian type, each of which is wholly responsible for the development of a Mendelian character. Castle's work shows that he has no such idea. He merely worked out the facts of color inheritance in rabbits, and, except for a brief reference in his closing paragraph about a possible mechanism for their explanation, gives no indication that he has any theory to explain them. He certainly does not commit himself to the de Vriesian theory. Castle has shown us that there are three kinds of pigments in the hairs of rabbits whether they should be there or not, and that the tendency, under normal conditions, to produce these pigments is hereditary; furthermore that these tendencies are separately and independently transmitted. The fact is that there is nothing in the scheme of color factors presented by Castle inconsistent with the facts of color production presented by Riddle, unless it be that they call for two or three more or less distinct oxidizing processes instead of only one. Even the view that there is only a single process involved is not excluded if we can find a mechanism operative in development that stops the oxidation partly at one stage and partly at another.

I agree with Riddle that the placing of the "uniformity-spotted," etc., factors on the part of Castle in the germs of rabbits as alternative factors is a virtual surrender of the whole theory of discontinuous variation. According to my view, this theory has never had any sound basis except as a result of irregularities in the behavior of chromosomes, and Mendelian facts are not dependent on any such theory or in any way related to it, as the writer has repeatedly pointed out. Professor S. J. Holmes has also pointed out the fallacy in the assumption that Mendelian phenomena necessarily prove the theory of discontinuous variation.

That there may be more than one oxidation process concerned in the development of color in organisms is shown by a number of facts cited by Riddle. He gives a table of oxidation processes in which the end reactions result in various colors. He further cites the fact that lipochromes and guanin may possibly be the source of color in certain amphibia.

The author attempts to explain the variability in the second generation of hybrids as a result of unstable equilibrium of oxidation processes in the first generation. According to his view each of the gametes represents a stable condition. The first generation may be a compromise between the stable conditions found in the two gametes. In the second generation there is a tendency to revert to one or both of the stable points. This view is hardly in keeping with observed phenomena. The regularity with which certain types appear and their subsequent behavior with reference to the transmission of hereditary tendencies indicate, apparently beyond question, that there is some such definite segregation as would result from the assumption that the chromosomes play an important part in the general processes of cell metabolism.

Riddle shows his lack of knowledge of Mendelian principles and facts in his reference to the real contributions which Mendel has made. "The really important Mendelian contribution being that certain definite characters (such as have according to my belief, rather general processes as a basis) of different races may be combined to form new fixed races" (with which we all agree). "The establishment of this last fact has been most commonly considered by Mendelians on the one hand a consequence of the laws of dominance (!) and segregation, and on the other hand as a strong argument for a 'representative particle' basis for these two sets of phenomena." There are some Mendelians who really do not believe there is any law of dominance, and there are many more Mendelians who do not believe in a representative particle theory at all. Here, as elsewhere throughout his paper, Riddle confuses Mendelism with de Vriesianism and Weismannism. The following quotation applies only to de Vriesians and Weismannians, not to Mendelians: "With an eye seeing only *particles* and a speech only symbolizing them there is no such a thing as the study of a *process* possible." Castle in his work on rabbits has no such particles in his mind's eye; his terminology does not imply them; he merely describes the facts of color inheritance.

While in this review of Riddle's most interesting paper the writer has been compelled to appear to combat him at almost every point, he is quite in sympathy with Riddle's point of view. The thing he has tried to combat is Riddle's confusion of Mendelian facts with de Vriesian hypotheses. The writer hopes in the near future to be able to present a theory of Mendelian inheritance which is independent of the idea of unit characters and wholly independent of the idea of discontinuous variation.

W. J. SPILLMAN.